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THE LARVAL DEVELOPMENT OF CHITONS (AMPHINEURA)

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Most species of chitons, as indicated by previous studies, develop in much the same manner as gastropod mollusks. Normally, the sexes are separate and during spawning periods the sex products are extruded into the surrounding sea water, fertilization being largely a matter of chance. The fertilized ova divide rapidly and in a period of a few hours hatch into free-swimming larval stages consisting of ciliated trochophores. In a few days to a week or more the trochophore starts to take on the form of an adult, developing a creeping foot and the beginnings of the shell structure. At this stage a larval chiton is said to "metamorphose" and moves to the bottom to carry on further development as a young individual with all eight plates or valves completely formed. While this is the usual procedure, there are exceptions upon which the purpose of this paper is intended to focus particular attention.

Because the literature on chiton development is scattered, a brief enumeration of studies made by both earlier and later workers in this field will be helpful. Although the spawning habits of chitons and their embryological and subsequent larval development have been reported by relatively few investigators, some of the earlier work has been thorough for the particular species studied.

Earlier workers dealt with *Ischnochiton cinereus* (Linné), a fairly common small chiton with a distribution in British and Scandinavian seas and extending into the Mediterranean. Some applied other species names because taxonomic relationships were not well understood at the time. Clark (1855), Lovén (1856), Garnault (1888), Schweikart (1905), Knorre (1925), Hoffman (1931), and

Thorson (1946) all worked with *Ischnochiton cinereus*. Other European students of chiton development include Kowalevsky (1833), who dealt with *Chiton polii* Philippi [= *Nuttallina (Middendorffia) cinerea* (Poli, 1791)]; Plate (1899–1901), who reported on the embryology of *Nuttallochiton hyadesi* (Rochebrune); Lyngnes (1924), who studied both *Ischnochiton cinereus* and *Lepidopleurus asellus* (Spengler); Thiele (1906), who investigated *Notochiton mirandus* (Thiele); and Hammarsten and Rundström (1925), who did an excellent piece of research on *Acanthochitona discrepans* (Brown). Christiansen (1954) reported on the life history of *Lepidopleurus asellus*. Her paper on the methods used and the results achieved represents not only an important contribution to the subject of chiton development, but also contains by far the best review of the subject to date.

Heath (1899) started the study of New World chitons with a detailed investigation of the development of *Ischnochiton magdalenensis* (Hinds) [= *Stenoplax heathiana* Berry]. He also studied the breeding habits and development of *Lepidozona mertensi* (Middendorff), *L. cooperi* (Dall), *Mopalia muscosa* (Gould), *Katharina tunicata* (Wood), *Trachydermon raymondi* (Pilsbry) [= *Cyanoplax dentiens* (Gould)], *Nuttallina thomasi* Pilsbry, and the giant chiton, *Cryptochiton stelleri* (Middendorff), all relatively common species in the vicinity of Stanford University's Hopkins Marine Station, where Heath lived and worked.

Metcalf's work (1892–93) on the Caribbean species *Chiton squamosus* Linné and *C. marmoratus* Gmelin was followed by that of Crozier (1918) on *Chiton tuberculatus* Linné, type species of the genus *Chiton*. Grave (1932) reported on the development of the western Atlantic species, *Chaetopleura apiculata* (Say); Okuda (1947) also worked with *Cryptochiton stelleri*. The most recent published report is by Thorpe (1962), who made a study of the spawning habits of a number of California species, including specific information on the larval development of *Mopalia ciliata* (Sowerby).

The investigations of all workers mentioned cover a total of 19 species, in 14 presently recognized genera, grouped into 7 families, which is a fairly representative coverage of the order Polyplacophora. Nearly all of the chitons studied have a developmental pattern consistent with that already briefly sketched. In a few instances, however, exceptions to the normal pattern have been found to occur.

Kowalevsky in 1883 and Plate in 1898 noticed deviations in the development of the larval stages based, respectively, on studies of *Ischnochiton cinereus* and *I. imitator* (E. A. Smith). Heath, reporting in 1905, called attention to similar deviations as a result of his work with *Cyanoplax dentiens* and *Nuttallina thomasi*, saying these species:

> . . . carry their young until they are in an advanced trochophore stage. These, to the number of about 200 in the case of *Trachydermon* [= *Cyanoplax*], are held

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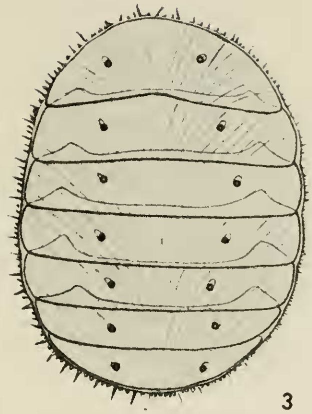

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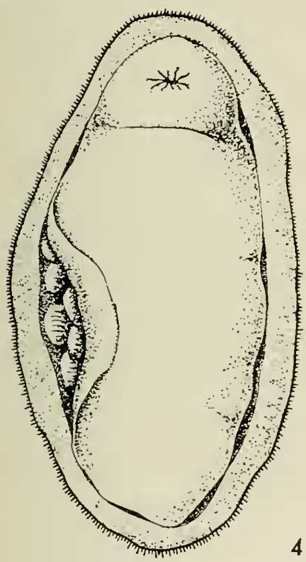

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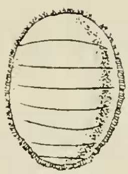

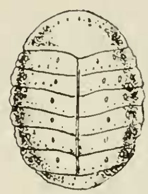

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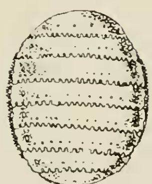

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Figure 1. *Hemiarthrum setulosum* (Dall). Female from below showing metamorphosed young in the branchial cavities. Length, about 10 mm. (After von Martens and Pfeffer.)

Figure 2. Same. Enlarged sketch of a single metamorphosed young animal. (After von Martens and Pfeffer.)

Figure 3. *Callistochiton viviparus* Plate. Enlarged sketch of a metamorphosed young specimen showing seven valves. (After Plate.)

Figure 4. *Schizoplax brandti* (Middendorff). Enlarged sketch of a female from below showing metamorphosed young in the branchial cavity. (After Kussakin.)

Figure 5. Same. (5a) Embryo at the stage of formation of the shell plates. (5b) Shell plates already formed but not fully developed. (5c) Young individual showing the divided intermediate shell plates and at a stage when ready to leave the mantle cavity of the mother. Length, about 0.75 mm. (After Kussakin.)

> in the mantle cavity on each side of the foot. Plate speaks of their extending over the neighboring regions of the mantle and to some extent on the foot, but in the present case this removal of the eggs from the mantle cavity never occurs until the animal has been disturbed. . . .
>
> *Nuttallina thomasi*, which breeds during the summer, carries its eggs in two rod-shaped masses, each approximately 80 eggs, held in the mantle cavity on each side of the foot.

Commenting on the dioecious condition in chitons, Heath (1907) found in his work with the development of *Cyanoplax dentiens* that this species is normally hermaphroditic and that the young "are brooded by the parent as in the case of *Chiton polii* [= *Nuttallina cinerea*], *Ischnochiton imitator,* and two or three other species."[1]

Iredale and Hull (1923, p. 191) state that: "One of us took specimens of *Heterozona subviridis* at King Island, Bass Strait, with clusters of eggs disposed along the outer margin of the foot." Dell (1962), while examining specimens of *Ischnochiton constanti* (Vélain) collected by the *William Scoresby* off Gough Island, Tristan da Cunha Group, in 40 to 60 fathoms, noted that "one specimen had a clump of eggs fixed to the branchial groove on each side . . ."

Martens and Pfeffer (1886) apparently were the first to observe a further deviation from the normal whereby the eggs and the hatched larvae were retained in the mantle cavity through metamorphosis, including the development of fully formed shell plates, a phenomenon they termed *brutpflege*. The species in this instance was *Hemiarthrum setulosum* Dall from Antarctic seas. In his discussion of this species in the Manual of Conchology (1892, pp. 19–21) Pilsbry does not mention its larval development. His figure 1 on plate 5 of the Manual is a 1 : 1 reproduction of Martens and Pfeffer's original figure, which shows the ventral side of a female specimen with metamorphosed young arranged along the sides of the foot under the girdle. This would have been made clear had Pilsbry used the original caption for this illustration. Also, Pilsbry did not include the enlarged drawing of a metamorphosed young specimen of *H. setulosum* supplied by Martens and Pfeffer. In consequence, both original illustrations are included herein as figures 1 and 2.

Plate, in 1898, was the next to report on a chiton actually brooding its young through metamorphosis. He also commented on the possibility that some might be viviparous. He named no species at that time but in his comprehensive work on the South American chitons contained in the *Fauna Chilensis*, published in 1902, he described *Callistochiton viviparus* as a new

[1] Heath mentions his success in raising the young of *Cyanoplax dentiens* and *Nuttallina thomasi* to sexual maturity by removing adults to isolated tide pools where the development of the young could be observed with facility over a considerable period of time. Christiansen used the method followed by Grave (1937) to induce larval development, moving the larvae to clean dishes with filtered sea water. Seven days after fertilization the larvae were supplied with the diatom *Nitschia closterior* as food, but her efforts to continue development of the young chitons after metamorphosis were unsuccessful.

species from Isla de Pacheros, 12 nautical miles from Coquimbo, Chile. His figure of the young stage after metamorphosis is reproduced in figure 3.

In 1910, Thiele added another species to the deviate list, *Sypharochiton nigrovirens* (Blainville). Barnard (in Ashby, 1931) notes that: "Thiele refers to the presence of young under the mantle (girdle) edge. The same fact was observed in the case of specimens collected by me at Smitswinkel Bay, False Bay, in July 1912. The young are about 0.75 mm. in length." Dell (1962) states that a specimen of *S. nigrovirens* from Saldhana Bay, South Africa, has fully developed young clustered under the girdle edge, about 33 on the left and 22 on the right side. The Spencer Thorpe Collection has a series of 62 specimens, preserved dry, from Kleinmond, South Africa, 20 of which have similar metamorphosed young. One specimen measuring 16.9 mm. in length has a total of 42, 23 on the right and 19 on the left side. The females bearing young range in length from about 9.5 to 18.5 mm., the young themselves being about 0.7 mm. long.

Another report of a chiton brooding its young was made in 1960 by Dr. O. G. Kussakin of the Zoological Institute of the USSR, Department of Hydrobiology, Leningrad. In this instance the species is the peculiar *Schizoplax brandti* (Middendorff), in which the intermediate shell plates are separated along the median line by a narrowly triangular wedge of cartilaginous material similar to that forming the hinge of a bivalve. This species occurs from the Okhotsk Sea, along the Aleutian Islands, and south on the Alaskan and Canadian side of western North America to at least as far as Graham Island off the coast of British Columbia. Kussakin's work was based on a year-round study of the development of *S. brandti* in the southern Kurile Islands in 1954–55. Because his paper may not be readily available to western specialists the somewhat revised English summary of it follows:

> A peculiar feature of the biology of *S. brandti* is the complete lack of a plankton larval stage; the whole development proceeds in the mantle (gill) cavity of the female from which the juveniles emerge with a completely formed shell resembling the adults. In this connection the development of *S. brandti* is considerably altered and simplified. Comparison of the development of this species with data available in the literature on other species indicates a trend in some chiton families toward a transition from a more complex to a more direct developmental process and toward viviparity.

Dr. Kussakin's drawings are indicative of the development of larval *Schizoplax* and they are reproduced with his permission as figures 4 and 5 of this report. Also, Dr. Kussakin has kindly furnished specimens in alcohol of *S. brandti* from the Kurile Islands, which contain both trochophore larvae and metamorphosed young. These have been deposited in the collection of preserved invertebrates in the Academy's Department of Invertebrate Zoology.

Mr. Spencer Thorpe informs me in connection with his study of the breeding habits of California chitons that he has found *Nuttallina thomasi* to be another species that mothers its young through metamorphosis, thus adding a fifth species to this category. Although Heath reported this species as carrying its eggs in the mantle cavity he made no mention of the stage at which the larvae emerged or were released from beneath the mantle.

To the five chiton species that follow a special development pattern, a sixth, may now be added, the particulars regarding which follow:

During a collection trip to Guadalupe Island, Mexico, in 1946, Mr. Woodbridge Williams made an interesting collection, principally in tide pools, of chitons and other species of mollusks (Smith, 1963). Among these was a large series of a small chiton that provides ample evidence of a propensity for mothering its young. Although original preservation of the specimens was in alcohol, unfortunately this particular lot was allowed to dry out. Careful microscopic examination of them disclosed that of 71 specimens, minute, white, perfectly-formed metamorphosed young were lying between the ctenidia and the side of the foot in 21 of them. Some of the specimens had from three to six young adhering to the dried-out animals, all with at least seven fairly well formed valves and an extremely narrow girdle with an outer fringe of well developed spicules. Although somewhat curled because of their dried-out condition, approximate measurements show a length of 0.25 to 0.35 mm., which is considerably smaller than for comparable young specimens of *Sypharochiton nigrovirens* owing, no doubt, to the much smaller size of adults of the Guadalupe Island species. In size and other characters they resemble a specimen figured by Christiansen for an early stage of *Lepidopleurus asellus* (fig. 6).

Examination under higher magnification of some of the Guadalupe Island specimens with metamorphosed young showed as many as six or eight additional roundish bodies between the sides of the foot and the gill rows. Undoubtedly these are trochophore larvae in various stages of development. One of them, removed after careful softening, showed some of the characters of a typical trochophore larva of *L. asellus* at the end of eight or nine days' development, with three ciliary processes or flagella still intact projecting from the anterior end (fig. 7).

At first, the above evidence seemed impelling reason to describe this unusual little chiton species as new. However, in discussing the situation with Dr. S. Stillman Berry of Redlands, California, he mentioned finding very young examples under the girdles of his *Lepidozona asthenes,* making a check with his species imperative. It happens that I collected the original lot of *L. asthenes* in 1916 at White's Point, Los Angeles County, California, consisting of about 70 specimens. The Academy's collection has 28 specimens from this type lot, enough to make an adequate comparison with the series from Guadalupe Island. Observation under a magnification of × 90 showed six with metamorphosed young still adhering to the under sides of the girdles in spite of the fact that in many specimens a crude attempt at removing the foot and the underlying viscera had been made.

Further comparison between the two series of specimens (Smith, 1963) led to the conclusion that the Guadalupe Island series unquestionably belongs to *L. asthenes* based on the criteria of valve sculpture and configuration, and on the relative size, placement, and striated nature of the girdle scales.

Still more evidence that this species mothers its young through metamorphosis was discovered recently while studying a series of small chitons taken off the coast of southern California by Dr. William E. Ritter and Professor William J. Raymond in the summer of 1901 under the auspices of the San Diego Marine Biological Association (a predecessor of the Scripps Institution of Oceanography). Among the various lots was one containing 18 specimens of *L. asthenes* collected intertidally at White's Point, the type locality. Three of these also had metamorphosed young beneath the mantles; one still has eight of them plainly visible on both sides of the foot of the dried animal, along with nine or ten unmetamorphosed larvae.

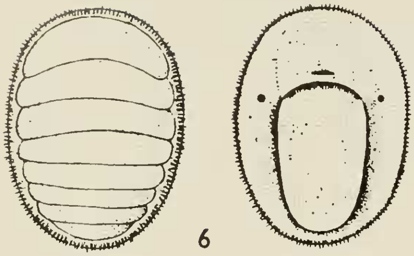
Development of Chiton Shell Plates

Although perhaps ancillary to the main subject of general chiton development in the early stages, the manner in which the shell plates form is of considerable interest. A number of accounts have been published about this but the reports of two or three specialists will serve to review our knowledge of the process.

Dall, writing in 1879 (p. 291), says: "The valves are first irregular, but increase from below, and deep notches, persistent in the adult, are formed on the front edges, one on each side. It will be seen that the valves are formed each in one piece, and by the coalescence of parts corresponding to the various areas of the adult valve. There are eight valves in all Chitons . . ." (fig. 8).

Heath's more detailed account (1899, Thesis, pp. 65–66) is as follows:

> The first clearly marked indications of the shell [in *Stenoplax heathiana*] occur usually about the fourth or fifth day when a band of somewhat clear cells appears parallel with and a little posterior to the prototroch. Very soon after another appears a short distance behind the first and the process is continued until seven such bands alternate with six narrow rows of darkly staining cells. . . . When treated with methyl green they stain intensely and this reaction continues as far as I have traced the development of the shell, when these cells come to occupy positions between the valves of the shell. The narrow bands of cells apparently but little differentiated which alternate with these mucous (?) cells gradually increase in breadth . . . and ultimately the calcareous portions of the shell appear above them.
>
> The calcareous salts are deposited in the cuticle covering the region of the shell and the presence of the tegmental sense organs (aesthetes) makes it evident that the first part of the shell to form is the tegmentum. The articulamentum appears later but the manner in which it forms is as yet unknown.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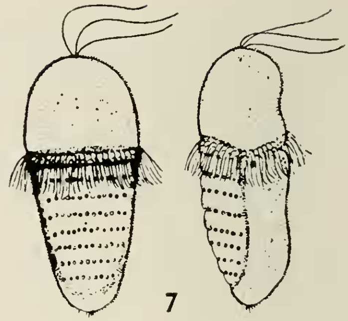
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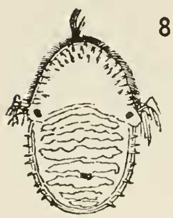
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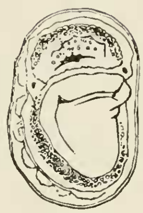
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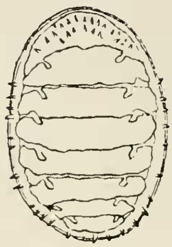
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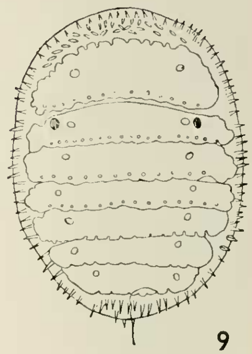
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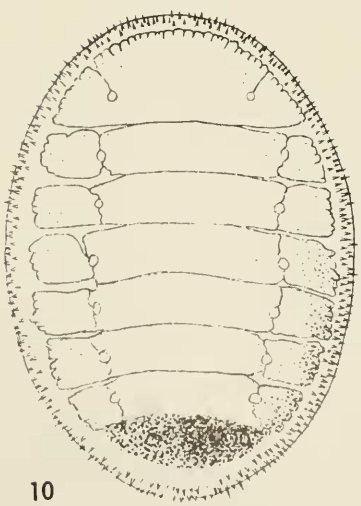
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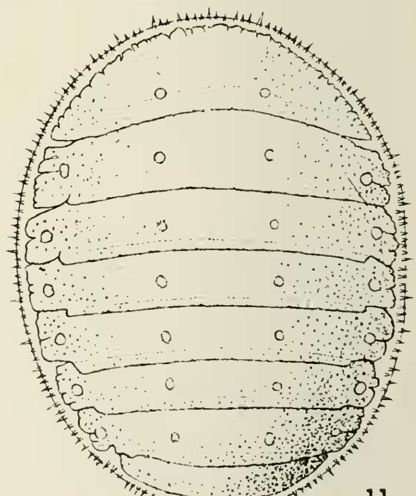
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Kowalevsky ('83) has accurately described the formation of the calcareous portions of the shell and *Ischnochiton* [i.e. *Stenoplax*] affords no further important points on this subject, (figs. 10, 11).

In *Lepidopleurus asellus* during metamorphosis, Christiansen says the rudiments of the shells extend into the dorsal region of the cephalic portion of the developing larva and the calcareous plates themselves appear very irregularly, each plate being composed of three parts. The eighth shell plate is the last to appear. In a nearly two-month-old larva the eight calcareous plates cover the back and appear to be well developed.

Thus, from these accounts, the formation of the first six shell plates seems reasonably clear, allowing for possible minor differences between species. There appears to be no specific information, however, on just how and when the last two (valves vii and viii) are formed. Plate's illustration of the metamorphosed larva of *Callistochiton viviparus* (fig. 3, herein) shows but seven complete shell plates. Likewise, Kowalevsky's figure of a well developed larva of "*Chiton polii*" shows seven (fig. 9), while his figure of a "young form" shows eight, with the eighth just beginning to develop. Christiansen says the tail plate (valve viii) of *Lepidopleurus asellus* is the last to appear. In my detailed examination of the metamorphosed young of both *Sypharochiton nigrovirens* and *Lepidozona asthenes*, however, the line of demarcation between the last two is extremely difficult to make out. For *L. asthenes,* in fact, some of the young appear to have only seven valves at the stage of development when they were collected, valve vii not being well developed.

Summary and Observations

To sum up from a survey of published accounts, the chiton species of the following list have been observed to deviate from the normal pattern of larval

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Figure 6. *Lepidopleurus asellus* (Spengler). Enlarged sketches of dorsal and ventral sides of a nearly two-month-old specimen after metamorphosis. (After Christiansen.)

Figure 7. Same. Enlarged sketches of dorsal and side views of a trochophore larva at 8¾ days. (After Christiansen.)

Figure 8. *Ischnochiton cinereus* (Linné). (8a) Dorsal view of larva. the valves beginning to be formed. (8b) Same. Ventral view, showing foot, and eyes at the sides of the head. (8c) Older individual, showing diminished size of the anterior tuberculate lobe, or head. (Dall, after Lovén.)

Figure 9. *Nuttallina* (*Middendorffia*) *cinerea* (Poli, 1791). Enlarged sketch of young form showing seven valves in process of formation. (After Kowalevsky.)

Figure 10. *Stenoplax heathiana* Berry. Much enlarged sketch of young stage at end of fourth day, showing fusion of the three portions of the valves. (After Heath.)

Figure 11. Same. Young stage fifteen days after hatching, with metamorphosis complete. (After Heath.)

development, with the females depositing their eggs in the branchial cavity and retaining them there at least to the trochophore larval stage:

Species	Family	Authority
Ischnochiton cinereus (Linné)	Ischnochitonidae	Thorson (1946) and others
" *imitator* (E. A. Smith)	"	Plate (1897–1901)
" *subviridis* (Iredale and May)	"	Iredale and Hull (1923)
" *constanti* (Vélain)	"	Dell (1962, 1964)
Cyanoplax dentiens (Gould)	"	Heath (1905)
Nuttallina cinerea (Poli)	Callistoplacidae	Kowalevsky (1883)
Chiton barnesi Gray	Chitonidae	Plate (1897–1901)

Species that mother their young through the final stage of metamorphosis, including the development of fully-formed shell plates are:

Species	Family	Authority
Hemiarthrum setulosum Dall	Lepidopleuridae	Martens and Pfeffer (1886)
Lepidozona asthenes (Berry)	Ischnochitonidae	This report
Schizoplax brandti (Middendorff)	Schizoplacidae	Kussakin (1960)
Callistochiton viviparus Plate	Callistoplacidae	Plate (1902)
Nuttallina thomasi Pilsbry	Callistoplacidae	Thorpe (unpubl.)
Sypharochiton nigrovirens (Blainville)	Chitonidae	Thiele (1910); Barnard (in Ashby, 1931); Dell (1962); this report.

The geographical distribution of these species, taken as a group, is worldwide. It does not conform to any particular pattern. Neither do their presently assigned systematic positions follow a pattern as the family-groups represented range from the more primitive (Lepidopleuridae) to species considered to have a high evolutionary development (Chitonidae).

The fact that a small number of totally unrelated species of chitons are now known to follow a type of larval development that deviates from the normal process indicates that studies of other species, whose life histories are unknown, should be investigated. Additionally, for some of the chiton species listed above, we need to be sure that the reported condition characterizes a species as a whole and is not merely an aberrant situation exhibited by a single or a few individuals induced, perhaps, by unusual or abnormal ecological conditions or other circumstances. Obviously, the possibilities for such studies are enormous when one considers that the total Recent chiton fauna of the world comprises something like 500 described forms. An interesting point, at present apparently undescribed, would be to determine specifically when and how the trochophore larvae of some species escape from the branchial cavity of the female as free-swimming veligers before metamorphosis occurs. Of equal interest would be the circumstances surrounding the eventual escape of the metamorphosed larvae of those species that mother their young through this stage.

This brief account of chiton development is dedicated with the respect and sincere good wishes of the author to his long-time friend and close associate, Dr. G Dallas Hanna, whose helpful encouragement and sound advice have been a constant source of inspiration over many years of personal contact. Such dedication is all the more fitting in view of Dr. Hanna's many contributions to the Academy's Recent mollusk collection over a long period, including the large suites of chitons he has collected from Pt. Barrow, Alaska, to Cape San Lucas at the tip of the Baja California peninsula.

Appreciation is due to Mr. Spencer R. Thorpe, Jr., of El Cerrito, California, for loaning his set of *Sypharochiton nigrovirens* for study, and to Mr. Maurice Giles, California Academy photographer, for his preparation of the illustrations.

Ashby, Edwin

1931. Monograph of the South African Polyplacophora (Chitons). Annals of the South African Museum, vol. 30, pt. 1, pp. 1–59, pls. 1–7, text figs. 1–2. August.

Berry, S. Stillman

1919. Notes on west American chitons—II. Proceedings of the California Academy of Sciences, 4th ser., vol. 9, no. 1, pp. 1–36, pls. 1–8. June 16. San Francisco.

Christiansen, Marit Ellen

1954. The life history of *Lepidopleurus asellus* (Spengler). (Placophora). Nytt Magasin for Zoologi, vol. 2, pp. 52–72, figs. 1–26. August. Oslo.

Clark, William

1855. On the phenomena of reproduction of the chitons. Annals and Magazine of Natural History, ser. 2, vol. 16, no. 37, pp. 446–449. London.

Crozier, W. J.

1918a. Growth and duration of life on *Chiton tuberculatus*. Proceedings of the National Academy of Sciences, vol. 4, no. 11, pp. 322–325. Washington.

1918b. Growth of *Chiton tuberculatus* in different environments. Proceedings of the National Academy of Sciences, vol. 4, no. 11, pp. 325–328. Washington.

Dall, William H.

1879. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. Proceedings of the United States National Museum, vol. 1, pp. 281–344, pls. 1–5. February 15–19. Washington. *Also in*: Scientific Results of the Exploration of Alaska, art. IV, pp. 63–126, pls. 1–5. February. Washington.

Dell, R. K.

1962. Stages in the development of viviparity in the Amphineura. Nature, vol. 195, no. 4840, pp. 512–513. August 4. London.

1964. Antarctic and Subantarctic Mollusca: Amphineura, Scaphopoda, and Bivalvia. Discovery Reports, vol. 33, pp. 93–250, pls. 2–6, text figs. 1–4. Cambridge University Press, London. [Amphineura, pp. 112–122.]

Garnault, P.

1888. Rescherches sur la structure et la developpment de l'oeuf et de son follicule chez les chitonides. Archives de zoologie expérimentale et générale, ser. 2, vol. 6, pp. 83–116. Paris.

Grave, Benjamin H.

1932. Embryology and life history of *Chaetopleura apiculata*. Journal of Morphology, vol. 54, no. 1, pp. 153–160, figs. 1–7. December 5.

1937. Culture methods for invertebrate animals. *Chaetopleura apiculata*, pp. 519–520. Ithaca, New York.

Hammarsten, O., and J. Runnström

1924. Ein Beitrag zur Kenntniss der Ontogenie der Placophoren. Archiv für zoologi, vol. 16, no. 19, pp. 1–5. Utgivet av K. Svenska Vetenskapsakadmien. Stockholm.

1925. Zur Embryologie von *Acanthochiton discrepans* Brown. Zoologische jahrbücher für anatomie und ontogenie der tiere, vol. 47, pp. 261–318. Jena.

Heath, Harold

1899. The development of *Ischnochiton*. Zoologische jahrbücher für anatomie und ontogenie der tiere, vol. 12, abth. f, pp. 567–656, pls. 1–5, figs. A–E. Jena.

Also published separately as: A Thesis submitted to the Faculty of the Department of Philosophy, in candidacy for the degree of Doctor of Philosophy, Department of Zoology, University of Pennsylvania, May 9, 1898, 90 pp., 5 pls., 5 figs. in text. Gustav Fischer, Jena.

1905. The breeding habits of chitons on the California coast. Zoologischer Anzeiger, vol. 29, no. 12, pp. 390–393. September 10. Leipzig.

1907. The gonad in certain species of chitons. Zoologischer Anzeiger, vol. 32, no. 1, pp. 10–12. July 23. Leipzig.

Higley, Rose M., and Harold Heath

1912. The development of the gonad and gonoducts in two species of chitons. Biological Bulletin, vol. 22, no. 2, pp. 95–97. January.

Hoffman, H.

1929–30. Polyplacophora. [In Bronn, H. G.] Klassen und Ordnungen des Tier-Reichs, bd. 3, nachtr. II, 1929, pp. 135–368, figs. 81–195; nachtr. III, 1930, pp. 369–453, figs. 196–210. [See especially, pp. 311–312, 362.]

1931. Beiträge zur Kenntnis der Chitonen. 1. Über die Fortpflanzung und Entwicklung von *Trachydermon cinereus* L. Zeitschrift für morphologie und ökologie der tiere, vol. 20, heft 4, pp. 719–732. Berlin.

Iredale, Tom, and A. F. Basset Hull

1923. A monograph of the Australian Loricates (Phylum Mollusca—Order Loricata). I. Systematics and structure. Australian Zoologist, vol. 3, pt. 5, pp. 186–194, figs. 1–4. December 18.

1927. A monograph of the Australian loricates (Phylum Mollusca Order Loricata). Royal Zoological Society of New South Wales, pp. i–xiii, 1–168, frontis. and pls. 1–21, text figs. 1–4.

Knorre, H. von

1925. Die Schale und die Rückensinnesorgane von *Trachydermon (Chiton) cinereus* L. und die ceylonischen Chitonen der Sammlung Plate. Fauna et Anatomia ceylanica, III, nr. 3. Jenaische Zietschrift für Naturwissenschaft, bd. 61, neue folge, bd. 54, pp. 469–632, taf. 18–35.

Kowalevsky, A.

1883. Embryogénie du *Chiton polii* (Philippi) avec quelques remarques sur le développment des autre Chitons. Annales musée d'histoire Naturelle Marseilles, Zoologie, vol. 1, no. 5, pp. 1–46. Marseilles.

Kussakin, O. G.

1960. Biological peculiarities of the Far Eastern mollusk *Schizoplax brandtii* (Middendorff). Zoological Journal of the Academy of Natural History of the U.S.S.R., vol. 39, no. 8, pp. 1145–1150, figs. 1–2. [In Russian, with a brief abstract in English.]

Lovén, S.
1856. Ueber die Entwickelung von *Chiton.* Archiv für Naturgeschichte, vol. 1, pp. 206–210. Berlin.

Lynges, R.
1924. Zur kenntnis der Eihüllen der Chitoniden. Skrifter Videnskabs-selskabet i Kristiania, 1923, nr. 20, pp. 1–12.

Martens, Eduard von, and Georg Pfeffer
1886. Die Mollusken von Süd-Goergien nach Deutschen Station 1882–83. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, 1885, II Jahrgang, pp. 65–135, pls. 1–4. Hamburg.

Metcalf, M. M.
1892. Preliminary notes on the embryology of *Chiton.* Johns Hopkins University Circulars, vol. 11, no. 97, pp. 79–80. April.
1893. Contributions to the embryology of *Chiton.* Johns Hopkins University Studies from the Biological Laboratory, vol. 5, no. 4, pp. 249–267, pls. 1–2.

Okuda, S.
1947. Notes on the post-larval development of the giant chiton, *Cryptochiton stelleri* (Middendorff). Journal of the Faculty of Science, Hokkaido Imperial University, vol. 9, no. 3, pp. 267–275. Sapporo.

Pilsbry, Henry A.
1892–93. Polyplacophora (Chitons), Manual of Conchology, vol. 14, pp. i-xxxiv, 1–350, text figs., 1–4. Philadelphia.

Plate, Ludwig H.
1897. Die Anatomie und Philogenie der Chitonen. Zoologische jahrbücher, supplement, bd. 4, pp. 1–243, pls. 1–12.
1898. Über primitiv Organisations verhältnisse, Viviparie und Brutflege bei Chitonen. Sitzungsberichte der Königlich Preussichen Akademie der Wissenschaften, XIV, pp. 213–217. Berlin. March 10.
1899–1901. Die Anatomie und Philogenie der Chitonen. Fauna Chilensis. Abhandlungen zur Kenntnis der Zoologie Chiles nach dem Sammlungen von Dr. L. Plate, bd. 2, heft 1, pp. 15–216 (Dec. 20, 1899); heft 2, pp. 281–600, pls. 12–16 (April 1, 1901). Zoologische Jahrbücher, supplement, bd. 4 and bd. 5, respectively. [For *Callistochiton viviparus* Plate, see bd. 2, pp. 154–163 and pl. 9, figs. 267–281.]

Schweikart, A.
1905. Beiträge zur Morphologie und Genese der Eihüllen der Cephalopoden und Chitonen. Zoologische jahrbücher, supplement, vol. 6, pp. 353–406.

Simroth, H.
1894. Ontogenie der Chitonen. [In Bronn, H. G.] Klassen und Ordnungen des Tier-Reichs, bd. 3, pp. 299–305, text figs. 33–36.

Smith, Allyn G.
1963. A revised list of chitons from Guadelupe Island, Mexico. The Veliger, vol. 5, no. 4, pp. 147–149. Berkeley. April 1.

Thiele, Johannes
1906. Über die Chitonen der deutschen Tiefsee-Expedition. Wissenschaftliche ergebnisse der deutschen tiefsee-expedition, auf dem dampfer 'Valdivia,' vol. 9, pp. 327–336. Jena. May 31.
1910. Polyplacophora, Gastropoda marina, Bivalvia. [In Schultze, L.] Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Südafrika ausgeführt in dem Jahren 1903–1905, bd. 4: Systematik und Tier-

geographie, lfg. 1–2, Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena, pp. 1–370, 14 taf.; lfg. 3, pp. 371–522, 9 taf.

Thorpe, Spencer R., Jr.

1962. A preliminary report on spawning and related phenomena in California chitons. The Veliger, vol. 4, no. 4, pp. 202–210, figs. 1–3, tables 1–5. Berkeley. April 1.

Thorson, Gunnar

1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). Meddeleser fra kommissionen for Danmarks Fiskeri og Havundersregeleser, Serie Plankton, vol. 4, pp. 1–523.